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Investigating *Ex Situ* Competitive Interactions in a Novel Fish Community with Implications for the Introduction of Sunfish (*Lepomis* spp.) in Headwater Streams

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Abiotic filters like high gradients or hydraulic drops play an integral role in excluding species from interacting with some headwater communities. When humans manipulate the ecosystems to install small ponds in the headwaters of river networks, they allow stocked species of fishes to escape and bypass these filters creating novel communities already under stress from other environmental changes. We investigated a novel headwater community to assess if and how escaped *Lepomis* spp. compete with a native headwater fish, *Chrosomus tennesseensis* (Tennessee Dace). We designed an *ex situ* mesocosm study to test the effects of exploitative and interference competition by two species—*L. macrochirus* and *L. cyanellus*—on *C. tennesseensis*. We observed strong intraspecific competition that exceeded the effects of both *Lepomis* spp. on *C. tennesseensis*. Although one individual was always a clear winner in intraspecific interactions, morphology at the beginning of the experiment could not explain why one individual was more successful than another. We also observed marginally higher growth rate in *C. tennesseensis* when *Lepomis* spp. were caged rather than free-swimming indicating that introduced *Lepomis* spp. likely impact headwater fishes through exploitative and interference competition in addition to the potential of predation at large size differences. More research is needed to understand the breadth and magnitude of potential problems posed by the unintentional introduction of stocked fishes to low-order streams.

ALTHOUGH headwater streams are dynamic in space and time, the communities that inhabit them have evolved adaptations and responses to the disturbance regimes of these systems (Creed, 2006). Human modifications to the landscape disrupt these disturbance regimes by altering the frequency, timing, and magnitude of disturbances (Lytle et al., 2001). The construction of small dams (Liu et al., 2014), riparian clearing (Rier and King, 1996), and introduction of non-native species (Hermoso et al., 2011) across the landscape affect fundamental characteristics of headwater stream networks by creating conditions that facilitate homogenization of stream fauna with widespread habitat generalists (Meyer et al., 2007). Introductions or invasions of widespread generalists create novel interactions (Marsh-Matthews et al., 2013; Ennen et al., 2020), which can synergistically interact with ongoing habitat modifications to disrupt long-established evolutionary patterns and contribute to the declines of endemic and vulnerable freshwater taxa (Rahel, 2002; McDonald et al., 2008).

Novel interactions have the potential to directly affect native species' population stability via predation, but they may also indirectly affect the behavior and success of individuals contributing to lower fitness and limited abilities to respond to environmental stochasticity (Jeschke et al., 2014; Marsh-Matthews et al., 2013). Describing the role that non-native species have in the declines of native species is important for determining if and what regulations are needed for landowners responsible for small-scale introductions of popular species. In the southeastern United States, small, constructed ponds are frequently stocked with centrarchids including *L. cyanellus*, *L. macrochirus*, *Micropterus dolomieu,* and *M. salmoides* (Smallmouth and Largemouth Bass; Huckins et al., 2000). The high connectivity of these ponds to local streams results in regular introduction of these fishes to local streams during high flow events. These events are common enough that these species are considered invasive outside of their native range (Couto d'Araújo et al., 2017). However, less attention has been dedicated toward understanding the role that these accidental introductions play within their native range.

Steep slopes and parallel drainage patterns have historically excluded centrarchids from low-order streams on the southern Cumberland Plateau (Baxter, 1997). Also, *Lepomis* spp. have an equilibrium-type life history and have few adaptations to overcoming barriers like waterfalls and steps, typically excluding them from high-gradient streams where headwater specialists thrive (Winemiller, 2005; Creed, 2006). However, small pond construction and subsequent fish introduction on the Cumberland Plateau have bypassed these geomorphic filters and allowed centrarchids to move into these high-gradient, low-order streams where highly specialized species like *C. tennesseensis* and *C. saylori* (Laurel Dace) are adapted (Baxter, 1997). Repeated introductions from upstream have the potential to disrupt the ecology of

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headwater stream communities. It is likely that these introduced and cosmopolitan species will compete directly for aquatic invertebrate prey and high flow refugia, and the aggressive foraging behaviors by introduced *Lepomis* spp. could also lead to avoidance behaviors by species like *C. tennesseensis*. Although the frequency of these introductions have not been documented here or elsewhere, 83% of streams with upstream dams surveyed by the authors have detected *Lepomis* spp. (S. Fix, unpubl. data).

The objective of this study was to evaluate the potential negative effects of exploitative and interference competition by introduced sunfish (*Lepomis* spp.) on a native headwater minnow in *ex situ* stream mesocosms. We hypothesized that introduced *Lepomis* spp. would negatively affect the growth of the native minnow. Secondly, we caged the introduced species to evaluate if they could induce negative effects in the absence of resource competition and physical interaction. For this study, we focused on the responses of *C. tennesseensis* as a native freshwater minnow that is isolated to drainages between the top of the southern Cumberland Plateau and the Sequatchie and Tennessee Rivers (Etnier and Starnes, 1993). This species has been used previously as a proxy for the federally listed *C. saylori* (Khudamrongsawat and Kuhajda, 2007; Fix, 2021). As two smaller *Lepomis* spp. more likely to succeed in low-order streams, we investigated the effects of *L. cyanellus* and *L. macrochirus*. We expected that the larger mouth and more aggressive foraging mode of *L. cyanellus* would contribute to larger negative effects relative to the less aggressive *L. macrochirus* (Etnier and Starnes, 1993). We also compared their effects when they were allowed to physically interact with *C. tennesseensis* and when they were prevented from interacting. If the effects of *Lepomis* spp. are minimized when they are prevented from physically interacting, it is likely that interference competition is a significant interaction between the two species.

MATERIALS AND METHODS

Twenty-nine individuals of *C. tennesseensis* were collected from Laurel Ford Branch in Spring City, Tennessee (35.679523, −84.890563; standard length ± 1 SE, 41±1 mm; mass ± 1 SE, 0.76±0.05 g) and ten individuals of *L. macrochirus* were collected from Richland Creek in Dayton, Tennessee (35.489872, –85.015169; 37±1 mm; 1.3±0.2 g) on 19 October 2020. Ten individuals of *L. cyanellus* were collected from Cupp Creek in Bledsoe County, Tennessee (35.490894, –85.179535; 34±2 mm; 1.8±0.1 g) on 21 October 2020. All fishes were weighed to the nearest 0.01 gram, and standard length (SL) was measured to the nearest millimeter.

Our experiment included five treatments that used two individuals per treatment. We evaluated an intraspecific pair of *C. tennesseensis* as our control that were allowed to interact physically. We compared this treatment to interspecific interactions between one *C. tennesseensis* and one *L. macrochirus* or one *C. tennesseensis* and one *L. cyanellus*. For each interspecific pair, we included two treatments that either allowed for physical interactions (free swimming) or prevented physical interactions by caging the individual of *L. cyanellus* or *L. macrochirus* in the pair (caged). Fishes were assigned to treatments based on size. For all free-swimming treatments, we only included fishes that were within 5 mm standard length of each other. Four intraspecific pairs and five interspecific pairs were randomly assigned to 24 independent stream mesocosms. The experiment lasted 46 days from 21 October 2020 to 7 December 2020. Fishes were recovered and immediately weighed and measured.

Mesocosms were 60 × 120 × 60 cm fiberglass tanks outfitted with a recirculating pump system. Each stream mesocosm drained into its own sump, creating independent replicates and base flows and temperatures similar to local streams and prior experiments (13.7±0.1°C; 40.5 L/min; Ennen et al., 2016; Cecala et al., 2020). Mesocosms were set up to replicate a small stream pool environment. Habitat within a mesocosm included gravel and sand substrate with an average water depth of 18.9±0.8 cm and two large rocks of approximately 800–1,000 cm^2. Caged *Lepomis* spp. were placed inside a 10 cm diameter PVC that was 15 cm long with window screen sealed with silicone on one opening and the other opening sealed with a window screen using a 10 cm metal clamp for easy access for feedings. Each fish was fed 25 g of thawed bloodworms twice per week. Caged fishes were fed inside of their cages, while free-swimming fishes were fed by pouring bloodworms into the mesocosm (25 g biweekly for caged treatments or 50 g biweekly for free-swimming pairs). Window screen was sealed over the top of the mesocosms to exclude predators and any aerial food supplementation.

We evaluated the effects of competitor identity (*L. cyanellus* or *L. macrochirus*) and interaction type (free swimming or caged) on the change in body condition of *C. tennesseensis* using a linear mixed effects model. We included mesocosm ID as a random effect. Body condition was quantified by the scaled mass index (henceforth referred to as body condition) that has been documented to be a more accurate metric representing body fat in small vertebrates (Peig and Green, 2009, 2010; MacCracken and Stebbings, 2012). We used package lme4 to perform our model and package emmeans to conduct *post hoc* evaluations using the Tukey adjustment for multiple comparisons (Bates et al., 2015; Lenth, 2019). For intraspecific treatments, many studies randomly select an individual to represent the treatment to minimize differences in variances among treatments (e.g., Cecala et al., 2020), yet when we observed our results, each intraspecific pair had an individual that greatly improved their body condition relative to their partner. Therefore, we included both individuals in our models. As a secondary analysis, we explored if winners and losers were different and if starting morphology predicted the future success of individuals in intraspecific pairs. Therefore, we performed a t-test and two linear regressions to evaluate if starting body size (standard length) and body condition (scaled mass index) influenced the outcome of intraspecific interactions as measured in this study using body condition. These analyses were implemented in R (R Core Team, 2020).

RESULTS

All *Lepomis* spp. and all but one *C. tennesseensis* survived the experiment. The mortality event was observed in an intraspecific treatment, and the surviving paired individual was included in the analysis as a winner. All *C. tennesseensis* increased in standard length (2.5±0.2 mm) and mass (0.35±0.03 g) during the experiment, and all surviving *C. tennesseensis* increased in body condition during the experiment. Treatment significantly affected the increase in body

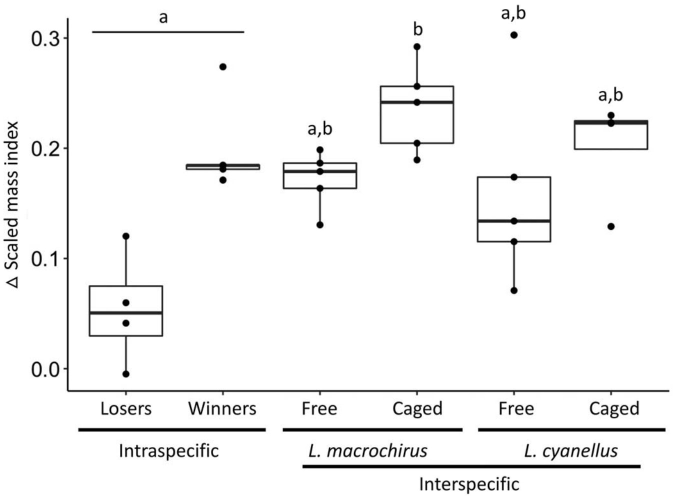

Fig. 1. Change in body condition of *Chrosomus tennesseensis* (quantified by the scaled mass index) in response to being housed with different fish. Individuals from intraspecific treatments were separated by mesocosm into losing and winning categories for comparison with interspecific treatments with *L. macrochirus* or *L. cyanellus*. Free-swimming individuals were allowed to physically interact and exploitatively consume prey, whereas caged individuals were allowed to communicate with visual and chemical cues, but were prevented from physically interacting or competing for the same prey. Letters indicate statistically significant pairwise differences using an alpha of 0.05.

condition ($F_{5,23} = 5.91$, $P = 0.001$; Fig. 1). We did not observe significant differences in the performance of *C. tennesseensis* between treatment fish species or between free-swimming and caged treatments though body condition was 1.26–1.37 times higher in treatments where treatment fishes were caged. The only marginally significant pairwise difference was observed between caged *L. cyanellus* ($t = 2.83$, $P = 0.089$) and those in intraspecific interactions, though low sample sizes ($n = 4$ or 5 per treatment) suggest that this is a marginally significant difference.

When we compared winners and losers of intraspecific treatments to each other, we observed a weakly significant difference between losers and winners of intraspecific pairings ($t = 3.90$, $P = 0.059$; Fig. 1). Linear regressions indicated that there were no significant relationships between initial standard length or initial body condition and the change in body condition that an individual experienced ($R^2 = 0.17$, $P = 0.272$; $R^2 = 0.03$, $P = 0.656$, respectively; Fig. 2A, B). The winner in intraspecific pairs was equally likely to have begun as either the larger or smaller individual and was statistically unrelated to the starting difference in initial body length (Fig. 2C).

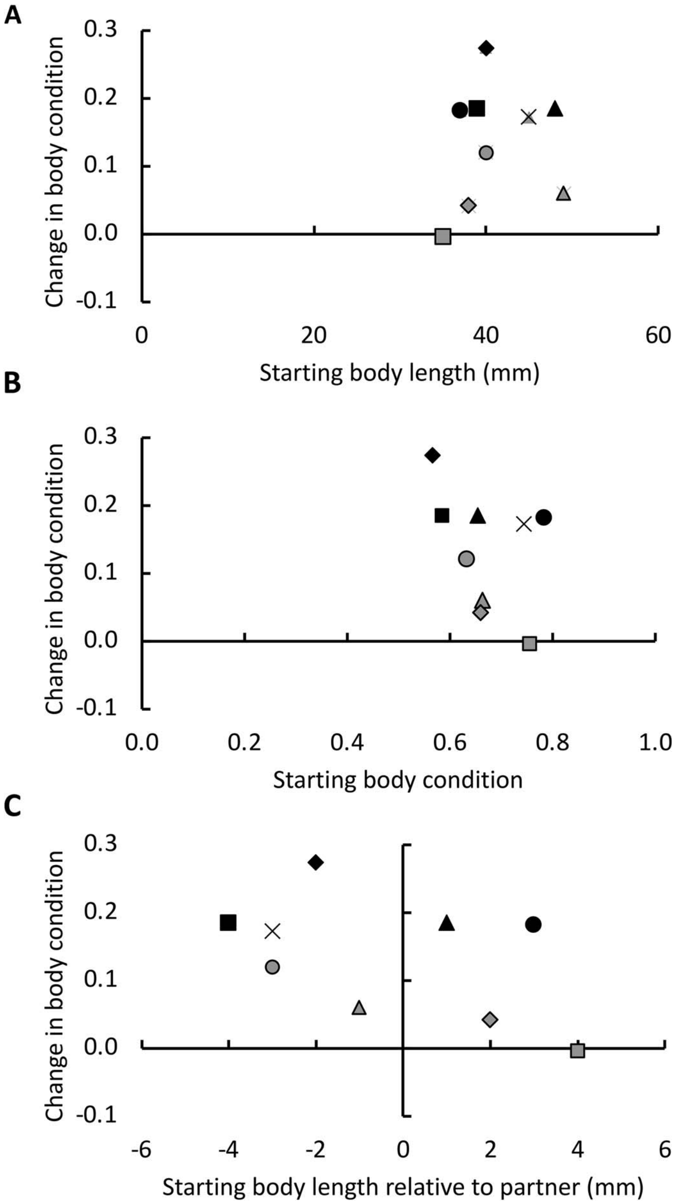

Fig. 2. Investigation of the relationships between the starting morphology of *Chrosomus tennesseensis*, including standard length (A), body condition (B), and length difference relative to the other individual in intraspecific pairs (C), and the change in body condition experienced over our 46-day experiment. None of these starting morphological measurements were associated with the outcome or success of individuals in intraspecific pairs (A, $R^2 = 0.17$, $P = 0.272$; B, $R^2 = 0.03$, $P = 0.656$). Body condition was quantified using the scaled mass index, and symbols indicate individuals within the same mesocosm. Black symbols indicate the winners of interactions, while the gray symbols indicate the losers of intraspecific interactions.

DISCUSSION

Overall, intraspecific competition had a stronger effect on performance of *C. tennesseensis* (Fig. 1). We observed a clear pattern of one individual in a pair performing well while another experienced significant negative effects from intraspecific competition. Although intraspecific pairs would be expected to have stronger negative responses from competition, we did not expect that individuals in interspecific pairs with species known to be highly aggressive would perform similarly to successful individuals in intraspecific pairs (Schoener, 1973). This pattern may indicate that intraspecific pairs may not be an appropriate control for interspecific interactions and that the degree of niche overlap with these two *Lepomis* spp. may not be sufficient to impair performance even when they are prevented from physically interacting (Bolnick, 2001). When individuals of *Lepomis* spp. were excluded from physically interacting with the *C. tennesseensis*, we observed a slight improvement of individual performance, suggesting that competition between *C. tennesseensis* and *Lepomis* spp. follows both exploitative and interference pathways (Cecala et al., 2020). Despite expectations that more aggressive *L. cyanellus* would have a stronger negative effect, we did not observe differences between the effects of the two species, which may be a result of using small and similarly sized individuals. Field observations indicate that *C. tennesseensis* and *C. saylori* are rarely found in pools with adult *Lepomis* spp. Therefore, we chose to use juveniles with small sizes that are more likely to co-occur with native species in these novel communities (Fix, 2021).

Intraspecific competition appears to be strong in *C. tennesseensis*, with each intraspecific pair resulting in a clear winner and loser in the interaction. Surprisingly, morphology was unable to predict the outcome of these interactions. Despite using natural densities of fishes (S. Fix, unpubl. data), intraspecific competition within the mesocosms was strong and resulted in slower growth of one individual (Kaspersson et al., 2013; Kornis et al., 2014). Because we used strict assignment criteria to minimize size differences among individuals, intraspecific pairs were likely to exhibit the largest niche overlap (Davey et al., 2005; Dehnhard et al., 2020), raising questions about the applicability of intraspecific controls to study interspecific competition (Rohde, 1991; Tarjuelo et al., 2017). Regardless, the clear dichotomy between winners and losers indicates that an unmeasured trait in these fish likely contributes to their success in intraspecific pairs. Although *C. tennesseensis* are not known to be aggressive towards one another, winners were able to gain significantly more weight by consuming more food and expending less energy. *Ex situ* conditions in the stream mesocosms may contribute to this pattern. Access to food was non-random and flow was turbulent towards the draining end of the mesocosm where flow was stopped by the downstream wall. Therefore, it may be that one individual excluded the other to this downstream area (= poor habitat), requiring inferior fish to expend more energy to stay in place while also being further from the food. Regardless of the proximate mechanism contributing to different energy dynamics, it is unclear what traits might maintain strict positioning within the mesocosms in the absence of territorial defense. Further investigation in intraspecific trait variation of *C. tennesseensis* is needed to elucidate the specific mechanism.

At similar sizes, *Lepomis* spp. could have non-consumptive effects on native headwater fishes (Sheriff et al., 2020). When we prevented physical interactions among fish by caging the other member of the pair, we observed marginally improved performance by *C. tennesseensis* (Fig. 1). Small *Lepomis* spp. likely use similar habitat and consume similar prey as *C. tennesseensis* because slow-moving pools are preferred habitat for all three of these species (Skelton and Schaefer, 2001; Hamed et al., 2008; Fix, 2021). However, if *C. tennesseensis* are unable to assess size-dependent predation risks, avoidance of *Lepomis* spp. could alter foraging and refuge-seeking behaviors (Marsh-Matthews et al., 2013; George et al., 2015). Alternatively, exploitative competition between similarly sized fish, regardless of species, could limit the performance of all individuals in a density-dependent manner (Kaspersson et al., 2013; Marsh-Matthews et al., 2013). In this instance, slower growth might be expected from all members of the community (Van Buskirk and Yurewicz, 1998). Ultimately, slower growth and/or lower densities of fishes could contribute to low resilience in native populations of headwater fishes (Brook et al., 2008; Capdevila et al., 2020).

Another potential explanation of our results is that the effects of *Lepomis* spp. are size-dependent. Invasive species tend to have larger impacts on native species when their interactions are predominantly predatory rather than competitive (Mooney and Cleland, 2001; Sax et al., 2002; Davis, 2003; Gurevitch and Padilla, 2004). *Lepomis* spp. at similar sizes to native headwater species may have limited impacts or impacts may require more time to observe, but at large size differences, *Lepomis* spp. might reduce or even eliminate successful recruitment through intraguild predation. This mechanism has been implicated in the decline and extirpation of *Fundulus julisia* (Barrens Topminnows) during invasion by *Gambusia affinis* (Ennen et al., 2020). *Ex situ* experiments confirmed that *G. affinis* regularly consume young-of-year *F. julisia* and that recruitment is absent in sites where *G. affinis* are present (Goldsworthy and Bettoli, 2006; Laha and Mattingly, 2007). Although extinctions are rarely attributed to invasive species, island habitats are the exception (Bellard et al., 2016). Headwater streams are not islands, but some share characteristics with islands—namely isolation by distance and physical barriers to invasion (e.g., waterfalls; Creed, 2006). Some headwater taxa already exhibit patchy distributions and limited gene flow due to other threats to habitat integrity and connectivity (Schultheis et al., 2002; Sterling et al., 2012), making the potential synergistic effects of invasion more detrimental to the long-term persistence of their inhabitants. In fact, anecdotal observations of *C. saylori* suggest that they are absent from pools where large *Lepomis* spp. are found, supporting this hypothesis of size-dependent effects (George et al., 2015; Fix, 2021).

By manipulating headwater streams to host small impoundments and stocking them with freshwater game fishes, humans interfere with geomorphic features that typically would exclude fishes like *Lepomis* spp. or *Micropterus* spp. from small headwater streams (Freeman et al., 2007). We predicted that the presence of *Lepomis* spp. in headwater streams would have strong negative effects on native fishes, but their effects were smaller than expected (Fig. 1). One potential explanation may be the naivety of *C. tennesseensis* toward *Lepomis* spp. that would not have historically co-occurred in the same streams (Carthey and Banks, 2014). Without experience co-occurring with *Lepomis* spp., anti-predator behaviors often observed in the presence of a potential predator may not be used, but evaluating this hypothesis would require additional behavioral testing to confirm (Sih et al., 2010). Despite this more recent history of interactions, *C. tennesseensis* were successful at increasing body condition in the presence of these native invaders. This study did not investigate size-structured threats to determine the primary mechanism by which *Lepomis* spp. could impact native headwater fishes (Claessen et al., 2002; de Roos et al., 2003; Werner and Peacor, 2003). Thus, more information is needed to understand the sizes of escaped fishes and how size-structured interactions between escaped fishes and native fishes affect local diversity in headwater streams. Indeed, little is known about whether *Lepomis* spp. can resist downstream drift in these streams and persist to become large enough to prey upon native species like *C. tennesseensis*. Regardless, overflow from headwater ponds likely results in continuous introductions of *Lepomis* spp. and *Micropterus* spp. to downstream communities where they would typically be excluded, and the ecosystem and diversity consequences of these repeated introductions is unclear (Huckins et al., 2000).

Understanding the interactions between native headwater fishes and fishes typically introduced to small man-made ponds is important because this interaction has been implicated in the decline of a federally listed species (George et al., 2015). *Chrosomus saylori* is closely related to *C. tennesseensis* used in this study. Although our study indicates that competition between similarly sized centrarchids may not cause harm to *C. saylori*, researchers have speculated that successful predation on *C. saylori* occurs when there are large size differences (George et al., 2015). Small, recreational ponds are regularly found on headwater streams (McCormick et al., 2010; Kirchberg et al., 2016; Webb, 2012), suggesting that escaped fishes could potentially have a more significant impact on headwater communities than previously understood (Sipple, 2016). We recommend that conservation and management planning for rare and threatened species consider the potential impacts of small, upstream dams (Gee et al., 1997; Jackson and Pringle, 2010). More research is needed to understand the processes leading to downstream escape of stocked fishes and the size distribution and fate of escaped fishes. This information will help researchers determine the significance and severity of this problem to minimize the homogenization of headwater fish communities and loss of rare species.

DATA ACCESSIBILITY

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